Of the four distinguishing characters of *Thaumatocrinus*, therefore, one appears in one or perhaps in two genera of *Comatulæ;* another is not to be met with in any *Comatula*, though occurring in certain stalked Crinoids; while the two remaining characters are limited to one family of the Palæocrinoids, one of them being peculiar to one, or at most two genera, which are confined to the Lower Silurian rocks.

Their reappearance in such a specialized type as a recent *Comatula* is, therefore, all the more striking.

IV. "On the Structure and Functions of the Eyes of Arthropoda." By B. Thompson Lowne, F.R.C.S., Lecturer on Physiology in the Middlesex Hospital Medical School, Examiner in Physiology in the Royal College of Surgeons, formerly Arris and Gale Lecturer on Anatomy and Physiology in the Royal College of Surgeons. Communicated by Professor Flower, F.R.S. Received March 30, 1883.

(Abstract.)

Three distinct forms of eye exist in the Arthropoda; the Compound eye, the Simple Ocellus, and the less known Compound Ocellus, common in larval insects, first described by Dr. Landois.

The relationship of the Compound eye to the Simple Ocellus is shown to be very distant, although I believe that these two types have been evolved from a common but very rudimentary primitive type. On the other hand, that between the Compound eye and the Compound Ocellus of a larval insect, is very close, the Compound eye being merely an aggregation of a great number of these ocelli, variously modified in the more highly differentiated Insects and Crustaceans. A fourth form of eye exists, in which the Ocelli are less closely united; this forms a connecting link between the compound eye and the compound ocellus. It is found in the Isopods, and may be conveniently termed the Aggregate eye.

The Simple Ocellus consists essentially of a pigmented capsule, behind a convex corneal lens, containing a cellular vitreous, which is separated from the retina by a fine fibrous membrane. The retina itself is a layer of Bacilla, comparable with those of Jacob's membrane in the Vertebrate, except that the highly refractive outer segments of the rods are turned towards and not away from the refractive media. The fibrous membrane, between the rods and the

group only. I cannot help suspecting that a better knowledge of this type will lead to its absorption into *Reteocrinus*.—P. H. C.

vitreous, is attached around its periphery to a structure which bears a strong resemblance to a ciliary muscle. This is enclosed in a ring-like sinus, which surrounds the ocellus almost as the canal of Petit runs round the lens of a Vertebrate. The vitreous is composed of a single layer of cuboid or prismatic cells, each with a nucleus near its inner extremity. These cells extend from the inner surface of the corneal lens to the outer surface of the fibrous membrane.

The Compound eye has a lenticular cornea beneath which the crystalline cones and great rods are placed. These are separated from the deeper nervous structures by a membrane comparable with the fibrous membrane of the Simple Ocellus; I have named this membrane the *Membrana Basilaris.*

The Membrana Basilaris is usually attached to the Cornea by an inflected ring of integument, the *Scleral Ring*, so that the Crystalline Cones and the Great Rods are entirely enclosed in a case. I have called all these structures the *Dioptron*, and have come to the conclusion that they are all Dioptric in function. They apparently correspond to the Cornea, Vitreous and Fibrous membrane of the Simple Ocellus.

The Membrana Basilaris, like the fibrous membrane, has a sinus around its periphery, and is connected with the inflected integumentary ring by fibres, which have a disposition similar to those of a ciliary muscle.

The Dioptron is nourished by Lymph Sinuses, which carry the circulating fluid from the Aorta* into the interior of the Dioptron and permit its exit into the common lymph spaces of the head.

Beneath the Dioptron is a nervous structure of great complexity; this I have named the Neuron.

The Neuron consists of a Retina, an Optic Nerve, and an Optic Ganglion.

The Retina is essentially a layer of rod-like bodies, Bacilla, supported by a delicate Neuroglia. The Bacilla are similar to the rods and cones of a Vertebrate in size, in form, and in structure, each has an outer highly refractive, and an inner protoplasmic segment. In some cases the outer segment is double, like that of the twin cones of fishes. In other specimens I have detected a *Lenticulus* between the segments. As in the Simple eye the highly refractive segments are turned towards the Dioptric media.

A layer of cells has been also demonstrated between the Basilar membrane and Bacilla; these in the majority of insects send pigmented fringes inward, between the outer segments of the Bacilla. The fringes are wanting in the diurnal flies, they represent the pigment layer of the Vertebrate retina.

I have spoken of the parts which underlie a single corneal

* I have so designated the anterior extremity of the dorsal vessel.

Lenticulus as a segment of the Dioptron. In many insects, especially in the larvæ, each segment has a distinct Retinula, consisting of a small bundle of Bacilla, which is connected with the ganglion by a distinct nerve enclosed in a separate pigmented sheath. I have named this form of retina *Segregate*. In other insects the retina is continuous over the inner surface of the Basilar membrane, but is connected with the deeper structures by a number of separate nerve bundles; whilst in the most highly developed Insects, a single decussating nerve connects a continuous retina with the ganglion. The ganglion consists of several nuclear and molecular layers, which are extremely like the corresponding layers of the retina of a Vertebrate.

All the structures of the Dioptron are developed from the cellular Hypoderm, whilst all the structures of the Neuron are formed from a solid papilla, or from a number of papillæ which are outgrowths from the Cephalic Ganglia, so that in this respect there is ground for a morphological comparison of the Dioptron with the dioptric structures, and of the Neuron with the nervous structures of the eye of a Vertebrate.

The Compound Ocellus of the larval insect is merely a single segment of a compound eye, with all the apparatus of the Dioptron and Neuron. I have used the term compound in relation to the refractive apparatus. The Neuron consists of a single bundle of Bacilla connected with the ganglion by a separate nerve bundle.

For several years I sought in vain for an explanation of the manner in which the compound eye could serve the purpose of vision. I discarded all the theories hitherto advanced, as being defective, and incapable of explaining the phenomena, consistently with the structure of the Great Rods.

Two years ago, whilst examining the recent eye of a small moth (*Pterophorus*), I was surprised to observe that the structure of the Great Rods was very different to anything with which I had previously been acquainted. The inner extremities of the Great Rods have been named Spindles, and are well known to present a very remarkable structure.

I first observed, in this moth, that the Spindles are, during life, large ovoid bodies, filled with transparent highly refractive fluid; the slightest injury gave rise to the escape of the fluid and left the Spindles in a shrivelled condition, the usual appearance of these bodies.

A further investigation has shown me that all compound eyes when uninjured have similar ovoid Spindles. These organs appear to act as magnifying and erecting lenses. Their anterior foci correspond to the position of the subcorneal images, and the posterior foci with the Bacillar layer of the retina.

It is well known that if an object-glass is placed in the reversed position beneath the stage of a microsoope, and the instrument is then focussed for its posterior focal plane, it can be used as a telescope. I regard the Dioptron as an aggregation of similar optical arrangements; the Corneal lens corresponds to the inverted objective, and the Spindle to the microscope.

I have made and given a series of measurements of the parts of an insect's eye in support of this view; the focal lengths of the corneal lenses, those of the spindles, and their relative distances, from each other, as well as the number and size of the corneal images are consistent with this theory. Therefore a continuous picture, *a mosaic of erect magnified central portions of the several subcorneal images*, falls upon the retina, and the sharpness of vision is not necessarily dependent on the number of corneal facets.

The complex modifications of the Dioptron appeared at first in many cases to offer insuperable objections to this view, and this necessitated a very careful reinvestigation of these structures, more especially in relation to the changes which they undergo in the preparation of sections for microscopic observation.

These researches have shown that many of the modifications observed are due to differences in the nature of the material of which the refractive elements are composed, not only in different genera and families, but even in the same species in different stages of development.

In many cases the refractive media consist of an oil-like fluid, which is decomposed or dissolved in the process of preparing the object for microscopic examination; in other cases the media consist in part at least of practically indestructible Chitin. And further the great elasticity of the parts gives rise to profound modifications the result of alterations of tension.

In the first, or introductory portion of my paper, I have reviewed the work of my predecessors with the object of showing the relation of previous observations to the theory which I have enunciated. The remainder of my communication is divided into four parts.

I. The Structure and Functions of the Dioptron.

II. The Structure and Functions of the Neuron.

III. The Development of the Compound Eye.

IV. The Morphology of the Eyes of Arthropods.

I. *The Structure and Functions of the Dioptron.*

In this portion of my paper the structure of the Dioptron is described, and its relation to the views I have adopted is discussed.

Perhaps the most important additions to our knowledge of this organ has been the discovery of the very important part played by the oil-like fluid already alluded to. This fluid is easily decomposed,

and resolved into a reddish granular precipitate and a transparent fluid, which mixes readily with water and saline solutions; it is blackened by osmic acid, and rapidly dissolved by ether, oil of cloves, and, though less rapidly, by alcohol.

A subcorneal lens has long been recognised in the eyes of Isopods, and has been regarded as a modified crystalline cone. Müller believed a similar lens to be present in the compound eyes of some insects. Of late this lens has been overlooked; I have, however, found that it really exists in the majority of Arthropods. It consists of the oil-like fluid just spoken of, enclosed in an elastic capsule. It gives the Cornea the peculiar brilliancy which it posseses during life. The fluid contents of the lens is permeated by a more or less dense stroma, which, when the oil is rapidly dissolved, by reagents, splits into four parts. These are the bodies described by Claparede as "*Semper's nuclei.*"

In some insects the lens can be isolated, and its capsule can then be ruptured by pressure on the thin cover-glass, so that the escape of the fluid can be actually observed. The empty capsules are then seen to be finely wrinkled, and usually torn by a single fissure.

In some insects the lens is developed from the cornea, in others from the outer portion of the crystalline cone.

The Spindles of the Great Rods also consist chiefly of the same refractive fluid, hence the profound modifications which they undergo when disturbed for purposes of investigation, or even as the result of *post mortem* change.

The formation of a subcorneal image as well as that of an erect image on the retina is discussed in this part of my paper, and the theory is shown by measurements to be in harmony with the actual conditions which have been observed.

The remainder of this part of my paper is occupied by a consideration of the principal modifications of the Dioptron.

I have recognised four distinct modifications of the Cornea, three of which exist in different stages of development in the cockroach. I have named these modifications,

I. Simple Continuous Cornea.

II. The Facetted Cornea.

III. The Kistoid Cornea.

The fourth modification is apparently confined, amongst insects, to the imago condition in the Gnats; in these the cornea consists of the crystalline cones of the nymph united to each other by a thin cuticular lamina. I have used the term lenticular to distinguish this form of cornea.

I have incorporated such knowledge as I have been able to glean with regard to the development of the cornea and subcorneal lens with this section of my paper.

The nature and modifications of the Crystalline Cone are next described; these afford an exceedingly difficult problem, on which further work will undoubtedly throw much light, especially in relation to the morphology of this organ. Some details with regard to the structure of the Great Rods are also added, which did not find a place in the general description of the Dioptron.

II. *The Anatomy and Functions of the Neuron.*

The Neuron consists of three parts—the Retina, the Optic Nerve, and the Optic Ganglion. The minute structure of these parts is fully described in this portion of my paper. The relation of the nerve fibres to the Bacilla and the Great Rods is also discussed. The optic ganglion consists of parts which are clearly comparable with the nuclear and molecular layers of the Vertebrate retina.

III. *The Development of the Compound Eye.*

The manner in which the Dioptron originates in the Hypoderm of the insect, as well as the nature and origin of the "Imaginal Disks," from which this structure is sometimes formed, is described. The development of the Neuron from the nerve-centres of the head presents features of extreme interest and importance, especially in relation to the phenomena of Ecdysis. The segregate retina of many larvæ is entirely replaced at the final Ecdysis by a newly formed retina, which is continuous, so that it appears as if a kind of internal Ecdysis affecting the epithelial elements of the nervous system occurs with the general integumental Ecdysis.

IV. *The Morphology of the Eyes of Arthropods.*

The final section of my paper is a short *résumé* of the Morphological relations of the different forms of Arthropod eye. These have been already alluded to in the commencement of this Abstract.

V. "Introductory Note on Communications to be presented on the Physiology of the Carbohydrates in the Animal System." By F. W. PAVY, M.D., F.R.S. Received April 5, 1883.

My last communication ("Proc. Roy. Soc.," vol. 32, p. 418) was entitled "A new Line of Research bearing on the Physiology of Sugar in the Animal System."

During the time which has since elapsed, I have been actively continuing my investigations in the direction started, and the results obtained give an entirely new aspect to the whole subject of the physiology of the carbohydrates in the animal system.